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Effects of food quality on growth and carcass composition in lambs of two breeds and their cross

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Abstract

The effects of food quality, breed type and sex (ram and ewe) on lamb growth and carcass composition, and their changes throughout growth, were measured. The three breed types were Scottish Blackface (B; no. = 24), Suffolk (S; no. = 28) and their reciprocal crosses (X; no. 33). The lambs had free access to a nutritionally non-limiting food, H, or a bulky food, L. Each lamb was scanned using X-ray computed tomography to measure the weights of fat, lean and bone in the carcass at three degrees of maturity (0·30, 0·45 and 0·65) in live weight. Live weight and food intake data were recorded weekly. Average daily gains in live weight (ADG) and carcass tissues, intake (ADI) and efficiency (EFF = ADG/ADI) were calculated for each lamb between degrees of maturity. Gompertz and Spillman functions were used to investigate relationships between weight and both time and cumulative food intake.

There was a breed by food interaction for fat and lean proportions ($P < 0·05$). Only on H was there a breed difference ($P < 0·05$) with S having less fat and more lean than either B or X, which did not differ from each other ($P > 0·1$). On food L there were no breed effects ($P > 0·1$). Across breeds, sexes and stages of maturity, food L caused lambs to have 0·810 as much fat and 1·063 as much lean compared with H ($P < 0·001$). There were breed by food interactions for ADG ($P < 0·05$) and EFF ($P < 0·01$). ADG on L was 0·72 of that on H for S, as compared with 0·79 for B and X. EFF on L was 0·463 of that on H for S, as compared with 0·586 for B and X. These were such that S was more sensitive to food effects on growth. The Gompertz and Spillman functions described growth well.

Keywords: *carcass composition, computed tomography, food intake, growth, sheep.*

Introduction

Lamb consumption has been declining over recent decades due, in part, to consumers' perception of lamb as being too fat (Woodward and Wheelock, 1990). It is therefore necessary that producers make breed, food and management decisions that tailor production systems to production environments and market requirements so that high quality lamb carcasses can be produced from available resources. As an aid to producers' decision-making, there is a need for more information on how different breed and food types affect lamb carcass and growth attributes and the importance of genotype by environment interactions. Previous studies have generally separately compared the effects of either breed (McClelland *et al.*, 1976; Taylor *et al.*, 1989; Friggens *et al.*, 1997) or food (Beauchemin *et al.*, 1995; Mahgoub *et al.*, 2000) on performance. However, there is little information on how these separate factors may interact to affect lamb growth and carcass composition under commercial conditions.

This study is part of a wider series which considers the performance of two diverse breeds (Suffolk, a terminal sire breed, and Scottish Blackface, a hill breed), and their crosses in a range of feeding environments including concentrates, dried forages and grazed pastures. The present study included these breed types on two concentrate foods of different quality. The breeds are known to vary widely in performance in a common environment (Emmans and Friggens, 1995) and, typically, the production environments in which the two breeds are kept differ in ways such that they produce

different responses in terms of growth and body composition at different stages of maturity (Croston and Pollott, 1994).

Traditionally, carcass composition has been studied using slaughter and dissection methods. However, X-ray computed tomography (CT) offers an accurate *in vivo* technique for estimating carcass composition (Young *et al.*, 2001). The technique can be used to study changes in carcass composition with growth, and the relationships between carcass composition, growth and food intake over time. Where comparisons between breeds and sexes are sensibly made at equal degrees of maturity in live weight, to remove at least in part the effects of differences in mature size and degree of maturity on the variables being examined (Taylor, 1980), the technique is particularly valuable.

This study had three main objectives: (i) to explore the effects of breed and food types on carcass composition, growth, food intakes and efficiency, (ii) to investigate how these relationships change during growth, and (iii) to test whether there are interactions present, particularly between breed and food.

Material and methods

Management

Ewes of the Scottish Blackface (no. = 19) and Suffolk (no. = 24) breeds were mated to four rams of each breed to produce lambs that were purebred Scottish Blackface (B), purebred Suffolk (S) or either of the two reciprocal crosses. Once born, lambs were reared either as twins or singletons. Triplet born lambs were cross-fostered to ewes with single lambs although no fostered lambs were used in the study. At birth, litter size, lamb weight, sex, and whether the lambing was difficult or not, were recorded. Within a week of birth, lambs were offered free access to a food of high quality called H (Table 1). Lambs were weighed weekly from birth. On reaching target weights of proportionally 0·20 of estimated mature weight (Table 2) or 8 weeks of age, whichever came sooner, they were weaned.

The estimate of mature weight for Scottish Blackface females came from Friggens *et al.* (1997) and that for Suffolk females from Lewis *et al.* (1998). The mature size of the crossbred females (88·0 kg) assumes a heterosis effect of 4% for mature weight in sheep (Nitter, 1978). The mature weight of males was assumed to be 1·3 that of females (Hammond, 1932).

At weaning, each lamb was allocated randomly to a feeding treatment within breed type, sex and half-sib sire family. Lambs on a given treatment were group penned and given the appropriate food. The two foods used were H, designed not to limit growth, or a bulky food (L), which was intended to restrict lamb performance (Table 1). Lambs on L were gradually introduced to the food during an adjustment period. On reaching a weight of approximately 1 kg heavier than their target weight (proportionately 0·2 of maturity, Table 2), the lambs were placed in individual pens (2·93 m^2) in a slatted shed and given *ad libitum* access to the allocated food. The food intake data started at this point.

Table 1 *Ingredients and chemical composition of the foods used*

	Nutritionally non-limiting food (H)	Bulky food (L)
Ingredient (g/kg)		
Barley	582·5	0·0
Dried grass	200·0	0·0
Oatfeed	0·0	628·9
Sugar beet	0·0	110·0
Hipro soya-bean meal	70·0	180·0
Fish meal	60·0	0·0
Molasses	50·0	50·0
Mineral and vitamin mix	37·5	31·1
Chemical composition		
Dry matter (DM; g/kg)	912	923
Crude protein (g/kg DM)	192	130
NDF (g/kg DM)†	225	595
AHEE (g/kg DM)†	32·6	13·7
Ash (g/kg DM)	75	73
NCGD (g/kg)†	780	430
Metabolizable energy (MJ/kg DM)‡	11·7	6·4

† NDF = neutral-detergent fibre; AHEE = acid hydrolysed ether extract; NCGD = neutral cellulase gamanase digestibility.
‡ Predicted from 0·014 NCGD + 0·025 AHEE (Thomas *et al.*, 1988).

Table 2 *Target weights (kg) for male (M) and female (F) lambs of each breed and their cross*

	Breed type‡					
	B		X		S	
Stage of maturity	M	F	M	F	M	F
Weaning	18·0	14·0	23·0	17·5	26·0	20·0
0·30†	27·0	20·5	34·0	26·0	39·0	30·0
0·45†	40·5	31·0	51·5	39·5	58·5	45·0
0·65†	58·5	45·0	74·0	57·0	84·5	65·0
Maturity	90·0	69·0	114·0	88·0	130·0	100·0

† Proportions of maturity in live weight at which lambs were computed tomography (CT) scanned.
‡ Breed types were purebred Scottish Blackface (B), purebred Suffolk (S) and both of their reciprocal crosses (X).

Table 3 *Numbers of male (M) and female (F) lambs in each treatment group*

	Breed type‡					
	B		X		S	
	M	F	M	F	M	F
Food H†	5	7	8	10	5	9
Food L†	5	7	6	9	5	9

† As described in Table 1.
‡ Breed types were purebred Scottish Blackface (B), purebred Suffolk (S) and both of their reciprocal crosses (X).

Pre-weighed amounts of food for the entire week were placed in individual buckets for each lamb. The troughs for each lamb were filled twice daily from their bucket with sufficient food to ensure its *ad libitum* availability. Food left at the end of the week was weighed and then, after retaining a small sample for analysis, discarded. All lambs also received 75 g of hay (crude protein 72 g/kg dry matter (DM); modified acid-detergent fibre 391 g/kg DM) daily. The allocation of the 85 lambs to treatment is shown in Table 3. The marked imbalance between the sexes reflected the relative lack of males born in that year. It was intended to have more of the crossbred lambs than of the purebred in order to compare the reciprocal crosses. As no differences could be demonstrated between the reciprocal crosses, the two groups were combined as 'the cross' (X).

Measurements

Live weights and food intakes, excluding hay, were recorded weekly. On reaching 0·30, 0·45 and 0·65 (end of test) of their estimated mature weight, each lamb was scanned using CT. Each lamb was scanned in cross-section at three sites: near the shoulder (sixth thoracic vertebra; TV6), along the loin (second lumbar vertebra; LV2) and at the hind leg (ischium, ISC). Areas of fat, lean and bone were measured from the scans at each of these three body sites.

Derived variables

Weights of fat, lean and bone in the carcass were predicted from a combination of the tissue areas given by the three CT scans and the lamb's live weight at scanning. The equations used for prediction came from previous calibration trials at the SAC-BioSS CT scanning unit on both breeds (M. Young, personal communication). The range of live weights in these trials for the Suffolk sheep was greater than the weights at which the animals were scanned in this experiment. For the Scottish Blackface sheep the range of weights in the calibration set was from 27·3 to 47·1 kg, which was less than the range of weights used in the experiment of 20·5 to 58·5 kg. The regression coefficients used in the predictions for S and B are shown in Table 4. In the absence of equations specifically for the crossbred, their weights were predicted from the mean of the coefficients of the two pure breeds.

Carcass weight was calculated as the sum of the predicted weights of fat, lean and bone in the carcass. Proportions of each tissue in the carcass (g/kg) for each lamb were then calculated, at each scanning event. Average daily gains of each tissue between the adjacent scanning events were calculated for each lamb. The data on intake and live weight were used to calculate average daily rates of gain (ADG; g/day) and food intake (ADI; g/day) between successive degrees of maturity (start of food intake recording to 0·30, 0·30 to 0·45 and 0·45 to 0·65). Food efficiency (g/kg) was calculated as EFF = 1000 × (ADG/ADI).

Statistical methods

In preliminary analyses, the residual maximum likelihood procedure (REML, Genstat 5 Committee, 2001) was used to fit a general linear model (GLM) to describe the derived variables. The removal of fixed

Table 4 *Coefficients of prediction equations used to predict fat, lean and bone weights (g) from computed tomography (CT) scan tissue areas and live weight for Scottish Blackface (B) and Suffolk (S) lambs*

Breed	Tissue	Constant	Live weight (kg)	Tissue area (mm^2)†			Residual s.d. (g)	R^2 (%)
				ISC	LV2	TV6		
B	Fat	−1330	58·9	0·094	0·244	0·188	208	90·1
	Lean	−1880	86·1	0·206	0·165	0·111	396	84·2
	Bone	−210	31·4	0·306	0·240	0·165	180	73·1
S	Fat	−3070	84·8	0·269	0·196	0·166	469	98·4
	Lean	−3860	114·0	0·247	0·175	0·105	656	96·3
	Bone	−252	34·9	0·309	0·472	0·136	305	89·1

† ISC = ischium; LV2 = second lumbar vertebra; TV6 = sixth thoracic vertebra.

effects, where significant, increases the power of the experiment. REML was used to fit fixed effects, as the data were unbalanced. Lamb sex (female or male), litter size (1, 2 or 3), rearing type (single or twin), weaning category (weight or age based), dam age (2 or 3 years), lambing difficulty score (assistance at lambing either was or was not required), and date of birth (as a linear covariate) were included in the model as fixed effects. Birth weight was included in the model as the deviation of an observation from the relevant breed type-sex mean, as a linear covariate. Treatment effects of breed and food type were also included. None of the fixed effects, apart from the lamb's birth weight, treatments and sex, explained substantial amounts of variation in any of the variables, and significance at $P < 0{\cdot}05$ was rare. In view of these results only birth weight, as a linear covariate, the treatment effects and sex were included in further analyses. Final GLMS were run to estimate the effects of breed type, food type and sex on the derived variables, and to test for the presence of interactions between these factors, with birth weight fitted as a covariate as described above.

Where a variable is measured at least three times on the same individual, residuals may well be correlated. A repeated measures analysis of variables was used to test this possibility where this was the case (Genstat 5 Committee, 2001). The variables analysed in this way were ADG, ADI and EFF, and the proportions of fat, lean and bone in the carcass. This method of analysis allowed the effect of stage of maturity on the variables, and the interactions of stage of maturity with the treatment effects, to be estimated.

Weight by time and cumulative food intake

For the males and females of each breed, and the cross, on H, the values of the parameters of the Gompertz growth function were estimated using treatment mean data for live weight, W, from birth through to 0·65 of maturity. The data used continued only to the time when the first lamb on a treatment reached the end of its recording period to avoid bias. To help avoid the high correlation between the estimated values of the two main parameters of the function in its normal form (Lewis *et al.*, 2002a), the actual form used was

$$W = (Z/B)\exp(-\exp(G_0 - B\,t)) \qquad (1).$$

The parameter Z, where $Z = (A\ B)$ with A being the asymptotic weight (kg) and B a rate parameter (per day), has a biological interpretation in that Z/e is the maximum daily growth rate (kg/day). The third parameter, G_0, is a transformed initial weight given by $G_0 = \ln(-\ln(W_0/A))$, where W_0 (kg) is the weight estimated at time $t = 0$. As there was no *a priori* reason to expect the sheep on L to grow at a fixed proportion of their potential, the function was not used for their data. The genetically scaled growth rate parameter was calculated as $B^* = BA^{0{\cdot}27}$ (Emmans, 1997).

Weight was plotted against cumulative food intake for the 12 breed-food-sex combinations to estimate the values of the parameters of the Spillman function (Spillman and Lang, 1924; Parks, 1982; Lewis *et al.*, 2002b and 2004). The form used was

$$W = W_0 + (A\text{-}W_0)\,[1\text{-}\exp(\text{-}k\,F)] \qquad (2)$$

where F is cumulative food intake (kg) from the start of treatment, and A (the asymptotic weight) and k are the parameters to be estimated. It was found that the estimates of A and k were highly correlated so the values of the lumped parameter $(A\ k)$ are also reported. In order to get direct estimates of the standard errors of $(A\ k)$ the Spillman function was reparameterized as $W = W_0 + (A\text{-}W_0)\ [1\text{-}\exp(\text{-}\ (s/A) \times F)]$ where s is $(A\ k)$. As with live weight, to avoid bias, the data used continued only to the time when the first lamb on a treatment reached the end of its recording period.

Carcass composition

It was expected (Taylor *et al.*, 1989) that breed and sex effects on carcass composition at a given degree of maturity would be small, if present at all, and that composition would change systematically with degree of maturity in weight defined as $u = W/A$. The model, a power function, used to describe the way in which carcass tissue proportion changed with u was:

$$y_{ijkn} = \mu + f_i + g_j + h_k + au^b{}_n + \varepsilon_{ijkn} \qquad (3)$$

where y_{ijkn} is the proportion of fat, lean or bone for lamb n ($n = 1, 2, 3, \ldots, 85$) on food f ($i = 1, 2$), of breed type g ($j = 1, 2, 3$) and of sex h ($k = 1, 2$) where u is stage of maturity, μ the overall mean and ε the residual error. The coefficient a is the linear regression of the tissue proportion on degree of maturity in weight. The allometric coefficient b (Emmans, 1988) indicates whether a tissue is early maturing ($b < 0$) or late maturing ($b > 0$) in relation to live weight.

Heterosis

Crossbred lambs are expected to be more heterozygous than their purebred parental breeds. Heterosis may therefore have affected the performance of X lambs in this study, a possibility that was tested by fitting the GLM:

Table 5 *Least-squares means of tissue proportions (g/kg) at each stage of maturity, and overall*†

Treatment effects	Food‡	Stage of maturity 0·30 Fat	0·30 Lean	0·30 Bone	0·45 Fat	0·45 Lean	0·45 Bone	0·65 Fat	0·65 Lean	0·65 Bone	Overall Fat	Overall Lean	Overall Bone
Breed type‡													
B	H	191	603	207	290	540	170	407	447	145	296	530	174
	L	113	641	246	234	574	193	343	502	155	230	572	198
X	H	178	608	214	298	538	165	394	461	145	290	535	175
	L	122	636	242	233	580	187	338	507	155	231	574	195
S	H	167	618	214	276	558	167	374	486	140	272	554	174
	L	117	638	245	244	575	181	339	511	150	234	575	191
Max. s.e.d.		13·58	11·01	8·73	11·06	9·27	4·51	11·83	9·76	3·65	10·17	8·45	4·27
Sex‡													
M		168	619	213	266	561	174	359	493	148	264	558	178
F		128	630	243	260	560	180	373	479	148	254	556	190
s.e.d.		7·35	5·97	4·73	5·98	5·02	2·43	6·41	5·29	1·97	5·51	4·58	2·32

† Food and stage of maturity affected all tissue proportions ($P < 0{\cdot}001$), as did their interaction for bone proportion ($P < 0{\cdot}001$). There was also a stage of maturity by sex interaction ($P < 0{\cdot}001$). The breed and sex main effects, however, were generally unimportant ($P > 0{\cdot}05$), with the exception of significant sex effects at 0·30 maturity for fat and bone proportions ($P < 0{\cdot}001$).
‡ As described in Tables 1 and 2.

$$y_{ijkmn} = \mu + f_i + h_j + s_k + d_m + sd_{km} + b(w_{ijkmn} - \bar{w}) + \varepsilon_{ijkmn} \quad (4)$$

where y_{ijkmn} is the value of the derived variable for lamb n ($n = 1, 2, 3, \ldots, 85$) that was on food f ($i = 1, 2$) and of sex h ($j = 1, 2$), with a sire of breed s ($k = 1, 2$) and a dam of breed d ($m = 1, 2$). The linear regression of the derived value on birth weight (w_{ijkmn}), where birth weight was expressed as a deviation from the mean birth weight of the lamb's sex and breed type (S, B or X) combination ($\bar{w}$), was also included in the model. β is the regression coefficient, μ the overall mean and ε the residual error. A significant interaction between sire and dam breed (sd_{km}) would indicate heterosis.

Results

Only for ADI and ADG (results not shown) was there an effect of heterosis. ADI was 1·06 times as high in the crossbred ($P < 0{\cdot}05$) between 0·30 and 0·65 of mature weight as the mean of the two pure breeds. For ADG the value was 1·11 times as high ($P < 0{\cdot}05$) between 0·45 and 0·65 of mature weight. There was no indication of heterosis for any of the tissue proportions ($P > 0{\cdot}20$).

Carcass composition

Breed, food and sex means are shown in Table 5. Food L caused carcasses to have more lean and bone, and less fat, than did food H across all stages of maturity ($P < 0{\cdot}001$). An interaction was present for carcass composition variables ($P < 0{\cdot}001$) between sex and degree of maturity. Female lambs were only 0·76 as fat as male lambs when 0·30 mature but thereafter the two sexes did not differ. There was also

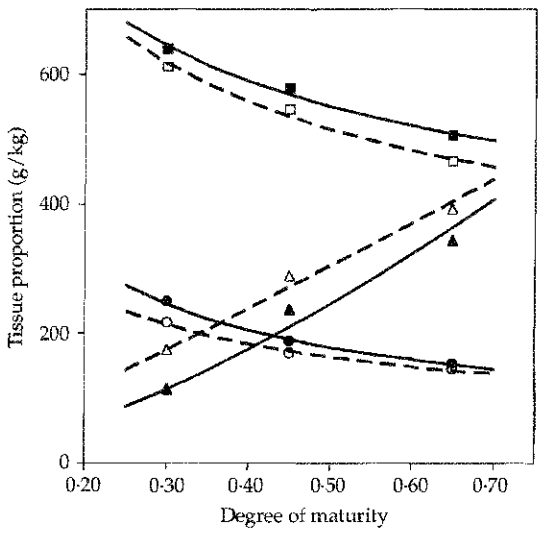

Figure 1 Changes in tissue proportions with increasing maturity as modelled by the allometric function (equation 3). The fits of the allometric functions for food H (- - - -) and for food L(——) are shown. The least-squares means for lean (■, □), fat (▲, △) and bone (●, ○) proportions when lambs were 0·30, 0·45 and 0·65 mature are also plotted. The maximum s.e. s (g/kg) were 4·23 for lean, 6·16 for fat and 4·00 for bone.

Table 6 *Least-squares means of gain in live weight (ADG; g/day), daily food intake (ADI; g/day) and food efficiency (EFF; g/kg) between stages of maturity, and overall*†

Treatment effects	Food§	Maturity interval: Start‡ to 0·30 ADG	ADI	EFF	0·30 to 0·45 ADG	ADI	EFF	0·45 to 0·65 ADG	ADI	EFF	Overall ADG	ADI	EFF
Breed type§													
B	H	296	1030	298	305	1491	205	180	1684	106	262	1403	203
	L	201	1323	162	265	1934	138	158	2295	68	206	1850	123
X	H	394	1234	333	380	1895	201	276	2201	125	350	1778	219
	L	274	1635	173	305	2546	120	249	3167	78	275	2445	124
S	H	431	1353	345	410	1994	208	332	2452	135	392	1929	231
	L	257	1853	139	311	2933	108	290	3573	80	284	2792	107
Max. s.e.d.		38·94	115·3	49·39	35·17	71·24	17·33	23·35	110·1	7·98	16·51	71·81	15·92
Sex§													
M		338	1630	227	352	2370	157	272	2799	99	320	2265	161
F		280	1181	257	307	1895	169	222	2325	98	269	1800	175
s.e.d.		21·09	62·18	26·75	18·98	38·54	9·36	12·60	59·37	4·32	8·95	38·97	8·69

† Food, maturity interval and their interaction affected all live measures ($P < 0·001$). The breed and sex main effects were important for ADG and ADI ($P < 0·01$), and breed for EFF ($P < 0·01$). There was also an interaction of breed with maturity interval and with food, and between food, maturity level and sex, for ADI ($P < 0·001$). An interaction between breed and food for ADG ($P < 0·05$) and EFF ($P < 0·01$) was also found.

‡ Start is when recording of food intake data began after the period of adjustment to the food treatment and corresponds to an average maturity of 0·20 of mature weight.

§ As described in Tables 1 and 2.

a breed by food interaction for fat and lean proportions ($P < 0·05$). Only on H was there a breed difference in fat and lean proportions ($P < 0·05$) with the Suffolk lambs having less fat and more lean than either the Blackface or the cross, which did not differ from each other ($P > 0·1$). On food L there were no breed effects ($P > 0·1$).

The power function (equation 3) showed as expected that fat is late maturing ($b = 1·2954$; s.e. = 0·0502; $P < 0·001$) and bone is early maturing ($b = -0·5693$; s.e. = 0·0195; $P < 0·001$) in relation to live weight. The model showed that lean matured significantly earlier than live weight ($b = -0·3312$; s.e. = 0·0116; $P < 0·001$)), but to a lesser extent than bone.

Food was the most important factor influencing change in proportion of each tissue over time, so the model was refitted for each food separately to determine how food type affected rate of maturing in tissues. Figure 1 shows the changes in fat, lean and bone proportions plotted against stage of maturity for the two foods used, as modelled by the power function. The data shown are averaged across the breeds and sexes. Fat was late maturing, more so on L than on H ($b = 1·515$ *versus* 1·091; s.e.d. 0·081; $P < 0·001$). Lean was early maturing, less so on L than on H ($b = -0·305$ *versus* –0·355; s.e.d. 0·019; $P < 0·01$). Bone was also early maturing, more so on L than on H ($b = -0·621$ *versus* –0·521; s.e.d. 0·033; $P < 0·01$).

Live performance

Average daily gains in live weight, average daily food intakes and food efficiency are shown in Table 6. Broadly, daily gains and intakes over all intervals increased with expected mature size; an exception was that S grew no faster than X on food L. Intake changed proportionally with stage of maturity in a way that was similar for all three breeds. Intake from the start of treatment to 0·30 was 0·66, and that from 0·45 to 0·65 was 1·20, times as great as that from 0·30 to 0·45. The repeated measures analysis showed no overall effects of either sex or breed on efficiency.

Food efficiency was, as expected, consistently less for lambs on L than for lambs on H ($P < 0·001$). The existence of breed by food interactions (see below) did not change the rankings of either breed or food. Lambs on L grew more slowly despite eating more food than lambs on H, although as lambs matured the difference in growth rate lessened while the difference in food intake increased. The repeated measures analyses for ADG, ADI and EFF confirmed these food by stage of maturity interactions ($P < 0·001$). Between start of treatment and 0·30

Table 7 *Least-squares means of average gains (g/day) in tissue weights between stages of maturity at which computed tomography (CT) scanning took place*

Treatment effects	Food†	Maturity interval: 0·30 to 0·45 Fat	Lean	Bone	0·45 to 0·65 Fat	Lean	Bone
Breed type†							
B	H	58·76	54·33	13·79	55·71	22·74	8·33
	L	40·60	47·36	11·80	41·64	29·46	7·04
X	H	85·77	73·40	14·50	84·49	42·67	14·48
	L	58·47	70·88	14·89	61·19	43·88	11·49
S	H	98·06	94·35	18·01	101·09	61·04	15·06
	L	67·89	77·65	15·52	70·76	60·71	14·96
Max. s.e.d.		6·091	6·461	2·255	7·185	4·739	1·098
Sex†							
M		71·84	72·92	15·98	69·20	48·58	13·45
F		64·68	66·46	13·52	69·10	38·25	10·33
s.e.d.		3·295	3·500	1·218	3·886	2·562	0·920
Significance							
Breed		***	***	*	***	***	***
Food		***	**		***		*
Sex		*	*	*		***	***
Food × sex						*	

† As described in Tables 1 and 2.

mature, lambs on food L had ADG, ADI and EFF values that were 0·651, 1·329 and 0·495, respectively, of those of lambs on H. By the period 0·45 to 0·65 mature, lambs on L had ADG, ADI and EFF values that were 0·886, 1·427 and 0·619, respectively, of those of lambs on food H.

Repeated measures analysis also showed an interaction between breed and food type for ADI ($P < 0·001$). The proportional increase in intake on L compared with H was less in Scottish Blackface lambs, and greater in the Suffolk lambs, than in the cross. There was also an interaction between food and sex for ADI ($P < 0·001$), where the sex difference in ADI was greater on food L than food H. The males ate 1·42 as much on L as on H; for females, the ratio was 1·35 (data not shown). Repeated measures analysis also found that interactions were present between breed and food for ADG ($P < 0·05$) and EFF ($P < 0·01$). The reduction in both growth rate and efficiency on L compared with H was greater for the Suffolk than for the Scottish Blackface and the cross.

Table 8 *Estimates of the parameters of the Gompertz function* $W = (Z/B)\ exp(-exp(G_0 - B\,t))$ *for lambs on food H*†

Breed type ‖	Sex ‖	A‡ (kg)	B (per day)	B^*§	Z (kg/day)	1000 Z/e (g/day)	Residual s. d. (kg)
B	M	68·28	0·01252	0·04214	0·8546	314	0·790
	F	57·98	0·01196	0·03751	0·6933	255	0·452
X	M	100·96	0·01059	0·03803	1·0692	393	0·687
	F	85·36	0·01031	0·03454	0·8803	324	0·443
S	M	125·47	0·00959	0·03568	1·2029	443	0·741
	F	112·26	0·00846	0·02934	0·9498	349	0·525

† Standard error values are not included as these may be misleading due to high correlations between estimates of parameter values. G_0 was estimated for the males as 1·035 (B), 1·086 (X) and 1·018 (S), and for the females as 0·913 (B), 1·034 (X) and 1·012 (S).

‡ The mature weight, A, was estimated as Z/B.

§ B^* was calculated as $B\,A^{0·27}$ (Emmans, 1997).

‖ As described in Table 2.

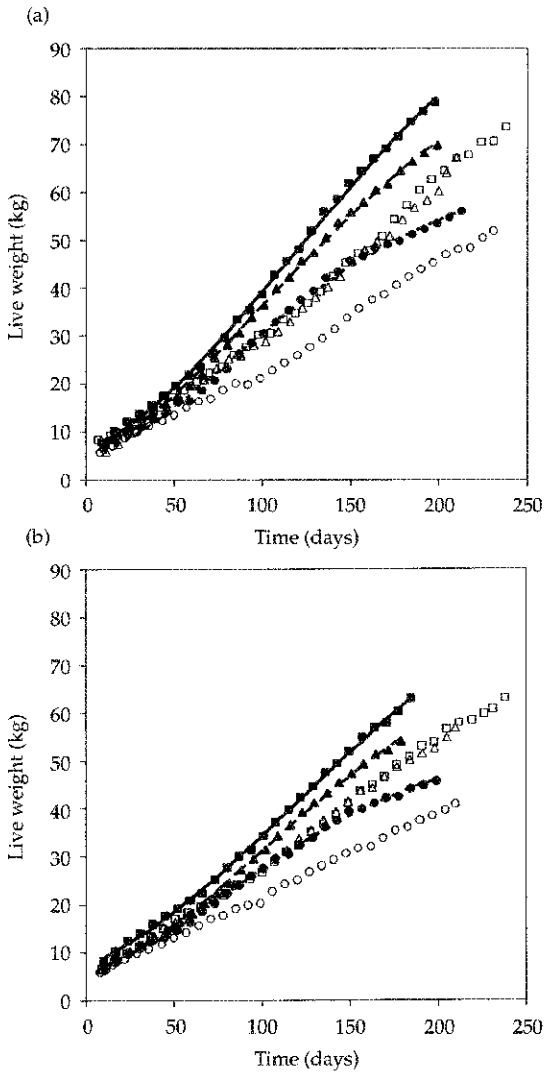

Figure 2 Live weight against time for (a) male lambs and (b) female lambs on food H: Suffolk (actual ■, predicted ——), Scottish Blackface (actual ●, predicted ·····), and their cross (actual ▲, predicted – – –). The data for the lambs on food L are also shown: Suffolk (actual □), Scottish Blackface (actual ○) and their cross (actual △).

Rates of gain of tissues

Table 7 shows average daily gains in fat, lean and bone weights between CT scanning events. As expected, breed affected gains in weights of all tissues for both intervals ($P < 0.05$). Food H caused lambs to gain fat considerably faster than did L during each interval ($P < 0.001$). Over the first interval, lambs on L gained lean at a slower rate than lambs on H ($P < 0.01$), but in the second interval there was no such effect. There was a small food by sex interaction ($P < 0.05$) for lean gain in the second interval.

Table 9 *Estimates of the parameters of the Spillman function* $W = W_0 + (A\text{-}W_0)\,[1\text{-}exp(\text{-}k\,F)]$ *for lambs on both food types*†

Breed type§	Food§	Sex§	A (kg)	k	$A\,k$‡	Residual s.d. (kg)
B	H	M	64·62	0·00633	0·4089	0·388
		F	54·30	0·00721	0·3916	0·272
	L	M	69·48	0·00322	0·2236	0·329
		F	54·47	0·00389	0·2117	0·339
X	H	M	90·37	0·00426	0·3849	0·347
		F	72·62	0·00532	0·3860	0·246
	L	M	88·50	0·00251	0·2224	0·558
		F	73·16	0·00310	0·2267	0·294
S	H	M	103·40	0·00406	0·4196	0·357
		F	85·03	0·00457	0·3884	0·219
	L	M	105·57	0·00202	0·2135	0·554
		F	81·63	0·00263	0·2147	0·330

† Standard error values are not included as these may be misleading due to high correlations between estimates of parameter values. W_0 (kg) was estimated for the males as 19·39 (B), 26·00 (X) and 27·74 (S), and for the females as 16·84 (B), 19·63 (X) and 22·74 (S).

‡ When directly estimated, the mean standard error for ($A\,k$) was 0·00722.

§ As described in Tables 1 and 2.

Gompertz and Spillman analyses

For lambs on food H the parameters of the Gompertz function are shown in Table 8. The growth trajectories generated from the fit of the Gompertz function for food H, and the mean actual data points for lambs on both foods, are shown in Figure 2a and b. The function fitted the data well for all groups; the residual standard deviation (r.s.d.) was between 0·443 and 0·790 kg. Growth was, as expected, clearly affected by breed and sex. Scottish Blackface lambs grew more slowly than Suffolk lambs, and cross lambs showed growth rates closer to those of Suffolk lambs than to those of Scottish Blackface. Male lambs grew faster than female lambs for all breeds.

Table 9 and Figure 3a and b show the estimates of parameters and curves generated by the Spillman function for lambs on foods H and L. Estimates of A and k were highly negatively correlated (around –0·73) and thus the lumped parameter $A\,k$ is a more robust descriptor of lamb growth by cumulative food intake. The fit of the Spillman function to the live weight by cumulative food intake data was generally good with residual standard deviations that were appreciably lower than those from the Gompertz

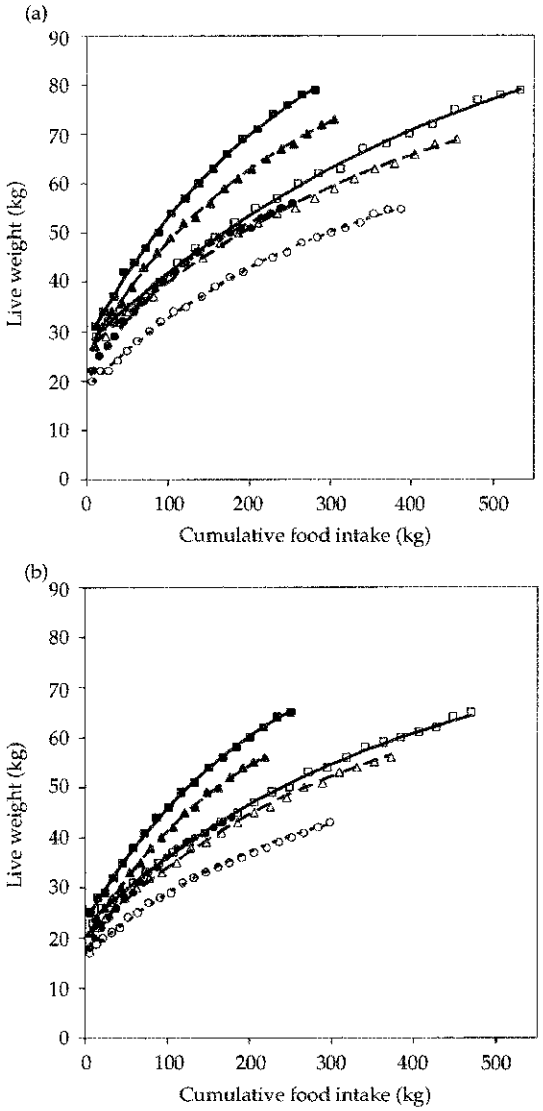

Figure 3 Live weight against cumulative food intake for (a) male lambs and (b) female lambs: Suffolk (actual ■, predicted ——), Scottish Blackface (actual ●, predicted ·····), and their cross (actual ▲, predicted - - - -), on food H, and Suffolk (actual □, predicted ——), Scottish Blackface (actual ○, predicted ·····) and their cross (actual △, predicted - - - -) on food L.

function (Tables 8 and 9). A clear effect of food type on lamb growth as a function of cumulative food intake can be seen in Figure 3. Lambs on L had lower A k values than lambs on H ($P < 0{\cdot}001$; Table 9). Differences in growth by cumulative food intake due to breed are less obvious on L than on H: the cross lambs had a growth pattern more similar to the Suffolk on L than H. This was not formally tested.

Discussion

CT scanning, an accurate *in vivo* imaging technique, was used to predict lamb carcass composition in the same animals as they grew. It has been shown to be able to have good prediction accuracies for carcass tissue weights (Sehested, 1984; Young *et al.*, 1996 and 1999). Young *et al.* (2001) found that for fat, lean and bone, the proportions of the variation accounted for were 0·99, 0·97 and 0·89, respectively, in meat sheep (e.g. Suffolk) and 0·92, 0·86 and 0·73, respectively, in hill lambs (e.g. Scottish Blackface). Compared with the long established method of serial slaughter (recent applications are described by Freking *et al.* (1999), Jones *et al.* (2002a) and Lewis *et al.* (2002b)), CT has the advantage of being able to be used to estimate carcass composition at intervals throughout the growth period in the same animal. As a result, fewer animals are required to achieve the same statistical power, the numbers of observations at each point is equal, and data can be collected from the same animals thus reducing error due to between-animal variation in body compositional change; however, the correlation between errors in the same animal is increased. Furthermore, growth and food intake data can be collected on the same animals over time, so the relationships between carcass composition and these variables throughout growth can be investigated.

Carcass composition

Little evidence has been found for between-breed variation in carcass composition in sheep at the same degree of maturity (McClelland and Russel, 1972; McClelland *et al.*, 1976; Butterfield *et al.*, 1983; Gaili, 1992; Oberbauer *et al.*, 1994). Apparent exceptions to the rule are the Texel (Wolf *et al.*, 1980; Kempster *et al.*, 1987; Jones *et al.*, 2002b) and the Soay (Thonney *et al.*, 1987b; Taylor *et al.*, 1989), both of which have been found to be leaner than expected. Hammond (1932) suggested that differences in carcass composition are likely to exist between those sheep breeds that have been subject to selection for meat traits and the less domesticated breeds that have not. Thonney *et al.* (1987b) and Taylor *et al.* (1989) reported that carcass composition appeared to be independent of mature size across six sheep breeds. The Soay, effectively a feral breed, was the exception. Wood *et al.* (1980) found no difference in carcass composition between ewe-type breeds (Clun Forest and Colbred) and meat-type breeds (Hampshire and Suffolk). Thus it is possible that breed differences in carcass composition may exist, over and above those accounted for by differences in stage of maturity and

mature size. Such differences may occur where breeds have been subject to different selection histories. On food L, at none of the stages of maturity used in the work reported here was there any evidence for differences in carcass composition between the Suffolk and Scottish Blackface breeds and their cross, in agreement with McClelland *et al.* (1976). However, on food H the Suffolk was significantly less fat and more muscular than the Blackface and the cross. The interaction between food and breed was significant indicating that generalizations about breed effects cannot safely be made across feeding environments.

The Scottish Blackface and Suffolk traditionally occupy different niches within the British sheep industry. The Scottish Blackface faces the climatically and nutritionally harsh environment of the hill ground, whereas the Suffolk generally has superior food and housing in upland and lowland flocks. In addition, the Suffolk has historically undergone selection for meat and carcass attributes. It could be expected, therefore, that these two breeds might well have different carcass compositions, at least in some environments. It might also be expected that these breeds would differ in their response to the two food types in this study as the food types that the Scottish Blackface and the Suffolk are usually exposed to, and may be adapted to, are different. The breed by food interactions present for both fat and lean contents support this hypothesis, with the Suffolk showing an advantage over the Scottish Blackface and the cross, in terms of lower fat and higher lean proportions in the carcass, only on food H.

McClelland *et al.* (1976) reported that there were no sex effects on carcass composition in sheep when compared at the same stage of maturity. Other evidence indicates that a sex difference exists in fat proportion once animals reach maturity (Taylor *et al.*, 1989) and at a range of other degrees of maturity (Wylie *et al.*, 1997; Lewis *et al.*, 2002b), with females being fatter than males. It is expected that a difference at any one stage of maturity would be seen at all stages of maturity (Emmans, 1988). We found that females had a lower fat proportion but only at the 0·30 stage of maturity. This was unexpected. Thompson *et al.* (1985) found that differences in body composition did exist between male and female Merino sheep compared at equal stages of maturity over a wide range of stages of maturity. Sex differences were shown to be greater at early and late stages of maturity, but at around 0·5 of mature weight sexes were similar in body composition.

Food type had an effect on carcass composition at all stages of maturity. Lambs on the food designed not to limit growth (H) were fatter at all stages of maturity than lambs on the bulkier food (L). It has been proposed that a higher growth rate *per se* causes carcasses to be fatter (Geenty *et al.*, 1979; Agricultural Research Council, 1980; Beuchemin *et al.*, 1995; Hall *et al.*, 2001). Butler-Hogg and Johnsson (1986), however, suggested that a higher growth rate could lead to leaner carcasses. The apparent contradiction may arise because the composition of the food changes the effect that growth rate has on carcass composition (Scales, 1993). Lewis *et al.* (2004) showed that lower food protein content decreased growth rate and increased fatness. Lewis *et al.* (2002b) found that a reduction in level of feeding reduced both growth and fatness. In this study the higher quality food had higher contents of both energy and protein and produced both higher growth rates and higher levels of fatness. There is thus no general relationship between growth rate and fatness.

Butterfield and Thompson (1983) suggested that the relative growth of carcass components would not be affected by rearing conditions. In contrast, Kempster *et al.* (1976) suggested that, in cattle, allometric coefficients would vary with feeding level. In our study on lambs, food quality had effects both on carcass composition at equal degrees of maturity in live weight and on the pathways to maturity for the different tissues. The allometric function described carcass composition well over the range of the data.

Live performance

Between breeds, body composition at a given degree of maturity was found to be independent of mature size. It is expected that much of the variation found between breeds and sexes in absolute growth rates and food intakes will reflect differences in mature size (Thonney *et al.*, 1987a). The large differences between breeds and sexes in the absolute rates of growth and food intake in this study were broadly in line with differences in mature size (Table 6). When scaled to $A^{0.73}$ (Taylor, 1980), breed and sex effects virtually disappeared. For example, the Scottish Blackface female (A = 69 kg) and the Suffolk male (A = 130 kg) had different absolute growth rates of 275 and 436 g/day between 0·30 and 0·45 of mature weight. However, when scaled to $A^{0.73}$ both values were 12·5 units.

The effect of food on efficiency was expected from the food compositions (Table 1) and reflected both slower growth and higher food intake on L compared with H. Food efficiency was independent of sex in this trial in agreement with other studies (McClelland *et al.*, 1973; Butterfield *et al.*, 1983;

Thonney *et al.*, 1987a). The same authors and Thompson and Parks (1983) also found no overall breed effects on efficiency. There was evidence that the breeds used here differed in their response to the different foods: efficiency was reduced in all breeds on L compared with H but to a greater extent in the Suffolk (ratio L : H = 0·463) than the Scottish Blackface (0·606). In the cross, the ratio was intermediate at 0·566.

The reduction in growth rate on L was less at greater degrees of maturity than at lower degrees of maturity. Overall growth rate on L was 0·651 of that on H from the start to the 0·30 stage of maturity; this ratio had increased to 0·886 for the interval from 0·45 to 0·65 of maturity. Food L was thus becoming less constraining as the lambs grew. In line with this, it was only during the 0·30 to 0·45 interval in degree of maturity that the rate of lean growth was lower on L than on H (Table 7).

The effects of breed and sex on growth (Figures 2a and b, 3a and b), supported by the Gompertz and Spillman analyses, are consistent with those expected from the differences in mature size. Lambs on food H grew faster and were more efficient than those on L as indicated by the values of the $A\,k$ parameter. This reinforces the conclusions that can be drawn from Table 6. The performance of the cross was intermediate between that of Suffolk and Scottish Blackface when food H was used. On food L, however, the growth of the cross was similar to that of Suffolk (Figure 2a and b). Growth rate in the cross was 1·07 times the mean of Scottish Blackface and Suffolk on H across degrees of maturity. On L the ratio was 1·13 indicating that the cross was, if anything, better able to cope with the poorer quality food than would have been expected from the mean of the two pure breeds. The breed by food interaction seen over the trial for ADG shows that, despite having higher growth than the other breeds on both foods, the Suffolk had an overall growth rate on L of 0·724 that on H, whereas in the Scottish Blackface and the cross this ratio was 0·786. This demonstrates that in this study, for growth rate, the Suffolk is slightly more sensitive to the food types than the Scottish Blackface and the cross.

The estimates of mature weight from the Gompertz function were 0·76 to 0·97 of the prior values given in Table 2 for all but female Suffolk lambs, where the ratio was 1·12. The estimates of mature weight from the Spillman function were also lower than expected, being consistently about 0·80 of their prior estimate. Estimates of mature weights in males were approximately 1·3 of mature weights in females as expected (Hammond, 1932). The underestimation of mature weight was probably a reflection of the data on live weights being curtailed at around 0·65 of mature weight.

The estimates of B^*, the genetically scaled growth rate parameter, in Table 8 are close to the standard mean for mammals of 0·03528 (Emmans, 1997). The Suffolk lambs used here had lower B^* values than expected from those analysed by Emmans (1997). A great majority of the lambs in this study did not come from lines that had been selected for lean tissue growth rate. Selection history is expected to affect B^*; the clearest case is in broiler chickens (Emmans and Kyriazakis, 2000). The females had lower B^* values than males, as shown in Table 8.

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